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STUDIES ON THE PLANT CELL.—VII.

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SECTION V. CELL ACTIVITIES AT CRITICAL PERIODS OF ONTOGENY IN PLANTS (*Continued*).

5. APOGAMY.

APOGAMY is the suppression of the sexual act and the development of a succeeding generation asexually. The term was first proposed by De Bary in 1878, following Farlow's ('74) discovery of the phenomenon in *Pteris cretica*. The succeeding generation may arise in one of two ways: (1) by the development of an unfertilized egg or gamete which is termed parthenogenesis, or (2) by some form of vegetative outgrowth from the sexual plant, a process which has been called vegetative apogamy. We shall not attempt to give a detailed account of apogamy in the plant kingdom but will confine ourselves chiefly to the consideration of a few detailed studies of recent months which have taken up the cell problems concerned. The cell problems naturally treat of the processes which may be substituted for the sexual act in ontogeny and the fundamental problems of the behavior of the chromosomes under these conditions.

Parthenogenesis has been known for many years among the thallophytes which furnish illustrations in a variety of groups. In the algæ we have the well known examples of *Chara crinita*, *Cutlaria*, *Dictyota*, some species of *Spirogyra* and *Zygnema*, and a number of types in the lower Chlorophyceæ and Phæophyceæ whose motile gametes will germinate like zoöspores should they fail to conjugate with one another. The recent studies of Williams (:04b) on *Dictyota* give the only observations which have been made on nuclear activities during the parthenogenetic development of eggs in any algal form and will be considered presently. The fungi furnish beautiful illustrations of partheno-

genesis in the Saprolegniales. Trow (:04) believes that some of these forms are sexual but there can be little doubt that the group as a whole is generally apogamous. There is probably much apogamy in the Ascomycetes and an almost entire suppression of sexual organs in the Basidiomycetes but no clear instance of parthenogenesis (*i. e.*, a development from a cell whose morphology is unquestionably that of an egg) is known in either of these groups.

Parthenogenesis is not known in the bryophytes and pteridophytes excepting for Marsilia (Shaw, '97; Nathansohn, :00). Although there is much apogamy in the pteridophytes, especially in the leptosporangiate Filicales, the new generation generally develops as a bud-like outgrowth on the prothallus (vegetative apogamy). There have been no nuclear studies on the parthenogenetic Marsilia but an interesting preliminary account has appeared announcing nuclear fusions in the apogamous development of Nephrodium (Farmer, Moore, and Digby, :03).

Parthenogenesis is now known in the spermatophytes for *Antennaria alpina* (Juel, '98, :00), several species of *Alchemilla* (Murbeck, :01a, :01b, :02; Strasburger, :04c), *Thalictrum purpurascens* (Overton, :02, :04), *Gnetum* (Lotsy, :03), a number of forms of *Taraxacum* (Raunkiaer, :03; Murbeck, :04), several species of *Hieracium* (Ostenfeld, :04a, :04b; Murbeck, :04), *Wikstrœmia indica* (Winkler, :05), and is suspected for *Ficus Treub*, :02) and *Bryonia dioica* (Bitter, :04). A number of cases of polyembryony were formerly considered examples of apogamy but are now known to be developments from the nucellus and consequently vegetative buds of sporophytic origin and entirely independent of gametophytic activities. The best known of these forms are *Funkia*, *Cœlebogyne*, *Citrus*, *Opuntia*, and *Alchemilla pastoralis*. Vegetative apogamy is illustrated in the development of embryos from antipodal cells as in *Allium odorum* (Tretjakow, '95; Hegelmaier, '97) or from the cells of the endosperm as in *Belanophora* (Treub, '98; Lotsy, '99). Synergids have been reported to form embryos in a number of forms but many of these have proved to be cases in which the synergid is fertilized by a sperm nucleus and not examples of apogamy. However, synergids are known to develop embryos apogamously

(or parthenogenetically if the antipodal be considered the homologue of an egg) in *Alchemilla sericata* (Murbeck, :02). A summary of the various types of vegetative apogamy, parthenogenesis, and sporophytic (nucellar) budding, supplementing a list of Ernst (:01) is given by Coulter and Chamberlain (:03, p. 221).

We will now take up the few investigations which consider the cytological details of parthenogenesis. That of Williams (:04b) on Dictyota is the only one treating of a lower type. It seems probable that parthenogenesis in Dictyota is in no sense normal and would not lead to mature plants, since the germination of unfertilized eggs in the cultures of Williams presented many irregularities. The spindles instead of being formed from asters with centrosomes are intranuclear in origin, multipolar, and very irregular in their form. As a result the 16 chromosomes become scattered and a cluster of daughter nuclei is formed containing varying numbers of chromosomes, sometimes one and sometimes several. It is clear in Dictyota that the fertilization of the egg results in the development of an aster with a centrosome which exerts a directive influence in mitosis preventing a scattering of the 32 chromosomes and conducting the mitosis in a normal fashion. Williams does not believe that the centrosome is introduced as an organized structure into the egg by the sperm but that it is formed *de novo* as a result of the increased metabolic activities present in the fusion nucleus as compared with that of the unfertilized egg.

There have been several important studies on parthenogenesis in the spermatophytes. Some of these papers while establishing the facts of parthenogenesis in various forms, give no details of nuclear history or behavior of the chromosomes. But the studies of Juel (:00), Overton (:04), and Strasburger (:04), present some very interesting data on the cytological features of parthenogenesis in *Antennaria alpina*, *Thalictrum purpurascens*, and several species of *Alchemilla*.

Several recent papers indicate that parthenogenesis may prove to be general in certain genera or even characteristic of large groups and therefore a far more widespread phenomenon than has been supposed. Raunkiaer (:03) (abstract in English in *Bot. Centralb.*, vol. 93, p. 81, 1903) proved by cutting off the

tops of young flowers that several species of *Taraxacum* produced normal seeds apogamously and concluded that the embryo must develop parthenogenetically since Schwere, in 1896, traced its origin from the egg. Ostenfeld (:04a, :04b) from failure to find pollen on the stigma of *Hieracium* and failure to make it germinate in a number of solutions, was led to try similar experiments to those of Raunkiaer in cutting off the anthers and stigmas of flowers. He found that a large number of species of *Hieracium* were able to set seed apogamously and he believed parthenogenetically but histological investigations were not made to establish the last point. The experiments of Raunkiaer and Ostenfeld are interesting as showing how a form by virtue of its parthenogenetic habits might become segregated and quite removed from the probability of hybridization. Murbeck (:04) in a short paper announced that the embryos in *Taraxacum* and *Hieracium*, developing from flowers whose stamens were cut out (as in the experiments of Raunkiaer and Ostenfeld) actually do develop from the egg cell and are therefore parthenogenetic. Murbeck also failed to find pollen tubes in the ovules where pollen had been applied to the stigma. Winkler (:04) reports that *Wikstrœmia indica* matures very little perfect pollen and produces its seeds apogamously, as proved by experiment. The embryos are stated to develop parthenogenetically from the egg but no details are given in this preliminary paper of the chromosome history. This group of contributions while very interesting, presents no data on the fundamental problems in a cytological explanation of parthenogenesis.

Murbeck (:01a) concluded for *Alchemilla* that true tetrads were formed previous to the differentiation of the embryo-sac but nevertheless found evidence that there were no reduction phenomena so that the nuclei within the embryo-sac contain the sporophytic number of chromosomes. Murbeck's evidence of tetrad formation was not satisfactory and in the light of recent studies of Strasburger (:04c) cannot be accepted. His view was, however, correct that there is no reduction of the chromosomes in the formation of such embryo-sacs as produced parthenogenetic embryos.

Juel (:00) gives a critical comparison of the development of

the embryo-sac in the parthenogenetic *Antennaria alpina* with *A. dioica* whose ovules are normally fertilized. In *A. dioica* the embryo-sac is one of a group of four cells (tetrad) which are formed through two successive mitoses (heterotypic and homotypic) showing the characteristic features of sporogenesis. A clear stage of synapsis precedes the first mitosis. The type of embryo-sac development in this form is then entirely normal. Not only are tetrads suppressed in the parthenogenetic *Antennaria alpina* but there is no trace of the heterotypic and homotypic mitoses in the embryo-sac. The number of chromosomes is very large (about fifty) and evidently the same as is found in other periods of the life history. There is then no reduction of the chromosomes during the formation of the embryo-sac in the parthenogenetic species and the egg and other nuclei in this structure have consequently the sporophytic number. There is no need of fertilization to bring the egg to a condition when with respect to chromosomes it is prepared to develop a sporophyte embryo. Juel (:04) notes certain peculiarities in the development of the embryo-sac of *Taraxacum officinale*. Tetrad formation is reduced to a single mitosis and this is not heterotypic, since there seems to be no reduction of the chromosomes. Details are not given.

Overton (:04) finds normal reduction phenomena in the pollen mother-cell of *Thalictrum purpurascens* which establishes the number of chromosomes to be 24 for the sporophyte and 12 for the gametophyte generations. These mitoses are thoroughly typical of sporogenesis being preceded by a synapsis stage. The development of the embryo-sac is of two types. In some cases a tetrad of four megaspores is formed from a megaspore mother-cell. The nucleus of this cell passes through a synapsis and the first mitosis is heterotypic showing the reduced number of chromosomes. The lower cell of the tetrad becomes the embryo-sac. But many embryo-sacs pass through a different history. There is no heterotypic mitosis and no reduction of the chromosomes which remain 24 in number. Thus in some ovules the mitoses of sporogenesis are omitted and true tetrads are not formed, with the result that the embryo-sac contains nuclei with the sporophyte number of chromosomes (24) in

place of the gametophyte (12). The details of the nuclear history in these embryo-sacs have not been followed but it is plain that their eggs have the requisite number of chromosomes to develop sporophyte embryos parthenogenetically. The varying proportions of parthenogenetically developed seeds which may be found on plants of *Thalictrum purpurascens* indicate that the suppression of normally developed embryo-sacs is not very firmly established in this form.

We now come to a recent paper of Strasburger (:04c) which is the most important contribution to the subject of parthenogenesis that has yet appeared. Strasburger studied a number of species of *Alchemilla* from the section *Eualchemilla*, the group which formed the subject of Murbeck's important discoveries. Most of the forms develop pollen in a normal manner and Strasburger was able to follow reduction phenomena in this process without difficulty. The nucleus of the pollen mother-cell passes through a synapsis followed by a heterotypic mitosis in which the structure of the chromosomes as bivalent elements is apparent. The bivalent chromosomes are in the reduced (gametophytic) number. Similarly Strasburger found that some species (*c. g.*, *Alchemilla pentaphylla*, *gelida*, and *grossidens*) formed embryo-sacs in a normal manner with the presence of a tetrad and a characteristic reduction division (heterotypic). But the development of the embryo-sac in apogamous species (*c. g.*, *Alchemilla speciosa*, *splendens*, and *fallax*) cuts out the two mitoses of sporogenesis and no tetrads are formed. The nucleus of the megaspore mother-cell emerges from synapsis with the sporophyte number of chromosomes and the first division which follows is a typical mitosis and not heterotypic. The embryo-sac then comes to contain a group of nuclei with the sporophytic number of chromosomes in place of the gametophytic and a parthenogenetic development of the egg takes place. Strasburger regards the parthenogenetic tendencies of *Eualchemilla* as associated with excessive mutations among these forms through which sexual processes are becoming displaced by apogamous methods of reproduction.

This clear evidence that the cause of parthenogenesis in *Antennaria*, *Thalictrum*, and *Alchemilla* lies in the suppression

of chromosome reduction during the formation of the embryo-sac seems to offer an explanation of other examples of apogamy presented by the embryo-sac. Thus apogamous developments of embryos from synergids as in *Alchemilla sericata* (Murbeck, :02) or from antipodals as in *Allium odorum* will not seem strange if reduction processes are suppressed in the production of an embryo-sac and its nuclei retain the sporophyte number of chromosomes. Such nuclei have in them the same potentialities of development as do those of the nucellus whose cells form embryos vegetatively and entirely independent of gametophytic activities in a number of forms (*e. g.*, *Funkia*, *Cœlebogyne*, *Citrus*, *Opuntia*, *Alchemilla pastoralis*, etc.). This type of apogamy from a gametophyte which retains the sporophyte number of chromosomes may be found to hold a very close relation to apospory for there is the same reduction or omission of the processes of sporogenesis as is found in that phenomenon. However, since we know nothing of the cytological events of apospory it is unwise at present to follow the speculation further.

The peculiarities of parthenogenesis in the spermatophytes do not seem so remarkable since the discoveries recorded above. It is not strange that an egg should form an embryo without fertilization when its nucleus contains the sporophyte number of chromosomes. The most remarkable feature in this suppression of reduction phenomena in *Antennaria*, *Thalictrum*, and *Alchemilla* is the possibility of developing an embryo-sac with nuclei in the number and arrangement typical of the female gametophyte and yet with the sporophyte count of chromosomes. The embryo-sacs with their contents have clearly the morphology of female gametophytes and must be so considered in spite of the fact that their nuclei contain twice as many chromosomes as usual. It is clear that the potentialities of sporophyte and gametophyte involve other factors besides those of the chromosome count. This is a very important conclusion because we have been accustomed to lay great weight on the number of chromosomes as the cause of sporophytic and gametophytic developments respectively. We must recognize the presence of other factors determining alternation of generations besides the chromosomes.

There are two types of parthenogenesis in plants : (1) that in the thallophytes where there is no sporophytic generation, and (2) that in higher forms when the life history is complicated by an alternation of generation. We know nothing of the cytological conditions in the first group including such types as *Chara crinita*, *Cutlaria*, some species of *Spirogyra* and *Zygnema* and numbers of the lower Chlorophyceæ and Phæophyceæ whose motile gametes will germinate like zoöspores should they fail to conjugate with one another. But since there is no reason to suppose that there are reduction phenomena at gametogenesis, the unfertilized gamete is fully prepared with respect to the number of chromosomes to continue the parent stock. Dictyota must be excluded from this list since the parthenogenetic developments here are abortive. In the second group parthenogenesis is likely to prove to be the result of a suppression of reduction processes during sporogenesis by which a gametophyte generation retains the sporophyte number of chromosomes and in consequence is prepared to dispense with sexual processes in the development of a new sporophyte. Parthenogenetic development in animals seems to be similar in its essential cytological features to parthenogenesis and apogamy in plants. There may be a suppression of reduction processes somewhat comparable to that discussed above, which takes place, however, at the time of gametogenesis, whereby the egg nucleus retains the number of chromosomes characteristic of the parent. Or, through a fusion with the nucleus of the second polar body the egg nucleus is brought back to the normal condition with respect to the number of chromosomes of the parent stock. We cannot, however, consider in detail the forms of parthenogenesis in animals. They have been recently treated by Blackman (:04b) in comparison with conditions in plants.

Apogamous developments which involve wholly or in part other elements than gamete cells and nuclei are likely to be established in a number of groups of the thallophytes. The author has long believed that the cystocarps of some of the Rhodophyceæ develop apogamously, basing his conclusions on certain general peculiarities of the group and more particularly on a study of *Ptilota* (Davis, '96). Three species of this genus

were investigated and no developments from the carpogonia were found, but the cystocarp in all cases arose from a cell near the base of the group of procarps. These conditions together with the rarity of male plants on the American coasts (none have ever been reported) give strong evidence for apogamy in *Ptilota*. There are a number of genera of the Rhodophyceæ where similar conditions seem to obtain and which lead one to suspect that apogamy may not be very exceptional. However, the subject has been very little studied.

As is well known, the Ascomycetes furnish numbers of illustrations where ascogonia have not been found or appear in what seem to be reduced conditions and even when accompanied by so called antheridial filaments these latter have not been established as functional. De Bary recognized the possibility of apogamy in the development of the ascocarps of these forms and very little critical study has been given to them since his time. The trend of investigations in this group has been towards the more interesting problems of the establishment of sexuality in a few well known forms (*e. g.*, *Gymnoascus*, *Sphærotheca*, *Pyronema*, *Monoascus*, and among the lichens and *Laboulbeniaceæ*.)

It is generally believed that no sexual organs are present in the higher Basidiomycetes (Autobasidiomycetes). But the recent studies of Blackman (:04a) in the Uredinales, taken in relation to the well known nuclear fusions in the basidium, preceded by a mycelium containing paired (conjugate) nuclei, make it seem very probable that former sexual processes in the Basidiomycetes have been replaced by a remarkable type of apogamous development of a sporophyte generation. Blackman has traced the origin of the paired nuclei in the Uredinales (*Phragmidium*) to a structure preceding the æcidium, a structure which seems to be the remains of a female sexual organ. We will take up this investigation presently. There is then much reason for believing that a sporophyte generation in the Basidiomycetes arises apogamously in the creation of the paired nuclei and terminates with their fusion within the teleutospore or basidium.

The leptosporangiate ferns have furnished some of the best

illustrations of apogamy. Since Farlow's discovery in 1874 of an asexual sporophytic growth from the prothallus of *Pteris cretica* the list of apogamous pteridophytes has steadily increased until now the phenomenon is known in perhaps 25 forms. Farlow's investigation was followed by an extended study of De Bary ('78) on a large number of forms in the Polypodiaceæ and resulted in the establishment of similar sporophytic outgrowths in *Aspidium falcatum* and *Aspidium filix-mas cristatum*. De Bary proposed the term *apogamy* ('78, p. 479) for the general phenomenon and distinguished two forms, *apandry* the suppression of the male sexual organs which results in a parthenogenetic development of the egg, and *apogyny* for the suppression of the female. Sadebeck in the following year reported apogamy in *Todea* one of the Osmundaceæ (Schenk's *Handbuch der Botanik*, vol. 1, p. 231, 1879) thus extending the phenomenon to another family. And later apogamy was found in *Trichomanes alatum* one of the Hymenophyllaceæ (Bower, '88) and in *Selaginella rupestris* (Lyon, :04, p. 287).

The most important recent contribution on apogamy in ferns is by Lang ('98, abstract in *Annals of Bot.*, vol. 12, p. 251). This paper presents an able discussion of the phenomenon in its relation to alternation of generations and adds the very interesting discovery of sporangia borne directly on prothalli that were grown from spores. These sporangia were found in clusters on a thickened lobe or process from the prothalli of *Scolopendrium vulgare ramulosissimum* and *Nephrodium dilatatum cristatum gracile*. The sporangia were perfectly normal in structure and they matured spores. It is probable that the process is itself sporophytic in character, *i. e.*, made up of cells with double the number of chromosomes of the true gametophytic portion of the prothallus, but cytological details are not known. Lang's study of the apogamous development of sporophytic buds on several forms of the Polypodiaceæ is the most detailed work on apogamy in the pteridophytes yet published. The apogamous growths appeared as the result of cultures which were watered entirely from below and exposed to direct sunlight, important departures from normal conditions surrounding fern prothalli. In all cases the prothalli developed normal

embryos when the conditions permitted of fertilization. We shall refer to some general considerations of Lang in our summary and conclusions on apogamy.

The spermatophytes present some exceedingly interesting examples of apogamous developments of embryos from nuclei within the embryo-sac other than the egg, as from antipodals (*Allium odorum*, Tretjakow, '95 ; Hegelmaier, '97) or synergids (*Alchemilla sericata*, Murbeck, :02) or nuclei in the endosperm (*Belanophora*, Treub, '98 ; Lotsy, '99) but in these cases the sporophyte number of chromosomes is apparently present through a suppression of the reduction phenomenon of sporogenesis in the development of the embryo-sac.

We will now consider two studies which describe nuclear fusions preliminary to the appearance of apogamy (Blackman, :04a ; Farmer, Moore, and Digby, :03).

Blackman's (:04a) observations on *Phragmidium* have cleared up to a great degree our understanding of the life history of the Uredinales. The chains of æcidiospores have been found to arise serially from "fertile cells" which form a group at the spot where an æcidium is to be developed. Each fertile cell has above it a sterile cell which, however, breaks down. The sterile and the "fertile cell" together may represent a female sexual organ, the sterile cell perhaps standing for the remains of a receptive structure similar to a trichogyne. The spermogonium consists of a large mass of antheridial filaments that abjoin sperms which are no longer functional. It is of course uncertain whether the "fertile cells" are morphologically the original female gametes since they may readily be other cells drawn into the process of apogamy. The "fertile cell" is stimulated to activity by the entrance of a second nucleus either from an adjacent hypha or from the cell below. The second nucleus does not fuse with the original nucleus in the "fertile cell" but the two come to lie close together as a paired or conjugate nucleus. The two nuclei of the pair divide simultaneously (conjugate mitosis) throughout a long series of nuclear divisions, beginning with the formation of æcidiospores and through the vegetative history which follows up to the production of the teleutospores where the members of the last pairs unite to form

the single fusion nuclei within these reproductive cells. There is much evidence that the period in the life history characterized by the presence of paired nuclei represents a sporophyte phase.

Blackman (:04a, p. 353) regards the process by which the second nucleus enters the "fertile cell," resulting in the conjugate nuclei, as a reduced form of ordinary fertilization. I have already pointed out in Section IV, "Asexual Cell Unions and Nuclear Fusions," what seem to me to be serious objections to the use of the term fertilization when it is clear that the second nucleus in the pair is morphologically not a gamete nucleus, and the subject was also taken up in the account of fertilization in the present section. Whatever may be the physiological interpretation of this remarkable phenomenon it seems to me clearly a substitute process for a former sexual condition and involves other elements than the original gametes and as such is a typical illustration of apogamy.

It seems probable that further studies in the Basidiomycetes will determine a similar origin for the paired nuclei preceding the basidium to that of Phragmidium but without any trace of former sexual organs at least in the higher groups. And these conditions must signify the complete disappearance of structures representing sexual organs and the substitution of an apogamous development of the sporophyte generation for the sexual act. In this connection the interesting nuclear fusions in the ascus are of great interest for they may hold relations to degenerate sexual conditions in the Ascomycetes.

Farmer, Moore, and Digby (:03) have reported some remarkable nuclear fusions preceding the apogamous development of the sporophytes of *Nephrodium*, which have many points of resemblance to the apogamous phenomena in the Uredinales just described. These authors find that cells of the prothallus from which the sporophytic outgrowths arise, become binucleate through the migration of nuclei from neighboring cells. The two nuclei may remain separate for some time or they may fuse at once. They regard the whole process "as a kind of irregular fertilization" by which the outgrowth destined to form the sporophyte becomes supplied with nuclei containing the double number of chromosomes. It seems to me unfortunate to asso-

ciate the term fertilization with this phenomenon, whatever may be the physiological significance of the nuclear fusions, because we are not dealing with gametes and there cannot be involved in the process anything of the long phylogenetic history of sexual differentiation in the group. We considered these matters in some detail in that portion of this section entitled "Fertilization."

With respect to the factors which determine apogamy it must be confessed that we are still in the dark. Lang's ('98) studies on fern prothalli, however, throw some light on the problem. In some twenty forms of the Polypodiaceæ apogamy resulted when the prothalli were kept from direct contact with the water (*i. e.*, were watered from below) and exposed to direct sunlight. When watered from above these same forms developed normal embryos from eggs. It is clear that the suppression of conditions which make fertilization possible (*i. e.*, water over the surface of the prothallus), possibly aided by sunlight which may cause irregularities of growth, induced the development of cylindrical processes from which the apogamous sporophytes arose and which bore sporangia in two forms. It seems hard to draw more precise conclusions from these experiments other than that the normal life history is checked at a critical period (fertilization) and the plant is forced into expressions of vegetative activity. The conclusions of Farmer, Moore, and Digby (:03) offer an explanation of how the developments may take on sporophytic characters through the fusion of nuclei in the tissues and the establishment of a sporophyte number of chromosomes.

Strasburger suggests that apogamy in *Alchemilla* may be the result of a weakening of sexual power associated with excessive mutative tendencies. This would seem to imply that exceptional vegetative activity, with the appearance of much variation under favoring conditions, may be combined with apogamy. It is of course a well known fact that a high degree of cultivation tends to lessen the fertility of a form unless guarded by careful selection. A weakened sexual fertility due to excessive vegetative activity is likely to be replaced by forms of vegetative reproduction. When the process of sporogenesis becomes so

reduced or modified that the female gametophyte retains the sporophyte number of chromosomes as in the embryo-sac of *Alchemilla* and *Thalictrum* the apogamous development of embryos is to be expected.

The discovery of apospory in such variable and perhaps mutating genera as *Alchemilla*, *Taraxacum*, and *Hieracium* suggests quite a new line of research with possibilities of a clearer understanding of the origin of mutations. It is very interesting that these widespread and successful genera should give evidence of such strong apogamous habits for it seems to indicate an evolutionary tendency in the higher plants of great significance. These forms with *Thalictrum* are representatives of three large, divergent and very successful orders (Ranales, Rosales, and Compositales) and it suggests the probability that apogamy will be found to be widespread in the spermatophytes. Its bearing on the establishment of extreme variations and mutations may be of the utmost significance for it is clear that the suppression of sexuality would remove sports and mutants at once from the swamping effects of cross-fertilization. The sudden appearance of mutants in some groups and their ability to hold true may indeed be found to rest on the establishment of apogamy in the form. This is at least a possibility which must be considered in cytological investigations on mutants and has not yet received attention.

The subject of apogamy touches another topic of importance, namely, the theory of *homologous* generations as contrasted with *antithetic* generations in comparisons of sporophyte with gametophyte. We shall not take up this discussion in detail here. It must have been apparent to the reader that the present treatment of the critical periods in the life history of plants is based on the conviction of the correctness of the latter view which has had the support of Celakovsky, Strasburger, Bower, Vaisey, and Klebs. The theory of *homologous* generations as held by Pringsheim and Scott is admirably discussed by Lang ('98) in connection with his studies on apogamy and also in a briefer note (*Annals of Bot.*, vol. 12, p. 583). Lang seemed inclined to the opinion that the facts of apogamy and apospory in ferns lent support to the theory of homologous generations since the

prothallus can so readily take on sporophytic potentialities and the sporophyte develop gametophytes vegetatively. But Lang recognized that the importance of this evidence would be minimized should it be found to depend on changes of nuclear structure. These nuclear changes have been established at least for apogamy, either in the suppression of the reduction phenomena of sporogenesis or by the substitution of asexual nuclear fusions for the sexual act, and the argument for antithetic alternation of generations seems to the writer stronger to-day than ever before.

6. APOSPORY.

Apospory is the suppression of all processes of sporogenesis and the development of a gametophyte generation directly from the sporophyte. The term was first proposed by Vines (*Jour. of Bot.*, 1878, p. 355) in a discussion of the life history of *Chara* and adopted by Bower ('86, '87) in a general treatment of the subject based on Druery's ('86a, '86b) discoveries of prothalli developed in place of sporangia directly upon the leaves of *Athyrium filix-femina* and its variety *clarissima*. The phenomenon of apospory is best known among the ferns where it has been most extensively studied but so far no cytological investigations have been published. Since apospory results in the development of a gametophyte generation (presumably with the gametophyte number of chromosomes) without the preliminary process of sporogenesis it becomes a very interesting problem to know just how this reduction of the chromosomes is effected.

Apospory is probably not uncommon in the mosses and has also been reported for the liverwort *Anthoceros*. The independent studies of Pringsheim ('76) and Stahl ('76) established the facts that pieces of the sporophyte stalk (seta) of *Hypnum*, *Amblystegium*, *Bryum*, and *Ceratodon* when placed on damp soil developed a protonema which in its turn produced leafy moss gametophytes. Stahl also found in *Ceratodon* that protonemata may arise from the capsule wall and Brizi ('92) discovered a similar development from the atrophied capsule of *Funaria hygrometrica*. Correns ('99a, p. 421) has confirmed the conclu-

sions of Pringsheim and Stahl in species of *Funaria*, *Hypnum*, and *Amblystegium* and obtained negative results in a number of other forms, and presents an excellent review of the subject. Lang (:01) discovered that small pieces of the sporophyte of *Anthoceros lævis* when laid on damp sand produced green outgrowths which took on the structure of young gametophytes and developed rhizoids. These aposporous gametophytes most commonly arose from subepidermal cells, but they may come from any layer of the cortex down to the archesporial cylinder. It seems probable that the mosses at least among the bryophytes are able to reproduce themselves apogamously without difficulty, when normal processes of sporogenesis are interfered with and if the sporophytic tissue is in contact with moisture.

The leptosporangiate ferns, however, furnish the most conspicuous illustrations of apospory as they do of apogamy. Indeed, the two phenomena are known to occur in the same form in a number of instances (*e. g.*, *Athyrium filix-fœmina*, *Nephrodium filix-mas*, *Scolopendrium vulgare*, *Trichomanes alatum*, etc.). Beginning with the discovery by Druery ('86a, '86b) of apospory in *Athyrium filix-fœmina* and its variety *clarissima* the list has steadily grown until now apospory is recorded for about ten forms. In Druery's forms the prothalli developed from arrested sporangia and the spore alone is left out of the life cycle. But Bower ('86) very shortly brought forward in *Polystichum angulare pulcherrimum* a form in which prothalli are developed as simple vegetative outgrowths from the tips of the leaves and the life history is thus shortened by the omission of both spores and sporangia. This condition is exactly analogous to the development of protonemata from vegetative cells of the sporophytes of mosses and *Anthoceros*. The following year Bower ('87) presented a very full account of the forms of *Athyrium* and *Polystichum* just described, and a general discussion of the phenomenon of apospory. Bower ('88) then extended the illustrations of apospory to two species of *Trichomanes*, of the Hymenophyllaceæ; Farlow ('89) reported it for *Pteris aquilina*, and Druery ('93) in *Lastrea pseudo-mas cristata* and ('95) for *Scolopendrium vulgare crispum*. The exceptional amount of fern variation both in nature and under cultivation has not been

generally appreciated and the studies on apospory and apogamy indicate that much of it is associated with these fundamental modifications of the life history (Druery, :01).

As to the cause of apospory we are as much in the dark as in the case of apogamy. The phenomenon is clearly associated in some forms with disturbances in the normal vegetative life of the sporophytes. This is particularly true in the cases of mosses and *Anthoceros* and has been suggested for the ferns. Thus aposporous developments in *Pteris aquilina* are from leaves which are generally smaller than the normal and whose margins are curled so that the leaf often appears somewhat withered and is easily recognized at a distance. Bower ('87, p. 322) is inclined to regard the phenomenon in the ferns as a sport and does not consider that it has deep morphological significance or that it offers serious difficulty to the acceptance of the theory of an antithetic alternation of generations.

As we have stated there have been no cytological studies upon apospory but there seem to be two possible explanations. That which is likely to suggest itself first calls for reduction phenomena at the time of the aposporous development by which the nuclei of the sporophytic tissues may come to contain the gametophyte number of chromosomes and are therefore capable of developing the sexual generation. But there is another possibility which has not yet been considered. We know for several of the spermatophytes (*Antennaria*, Juel, :00; *Thalictrum*, Overton, :04; *Alchemilla*, Strasburger, :04c) that the processes of sporogenesis may be suppressed and yet a structure be developed with the morphology of the gametophyte generation. Thus the embryo-sac will contain the usual number of nuclei grouped in the typical manner but these nuclei still have the sporophyte count of chromosomes. It seems probable then that the development of a gametophyte may result through an interference with the normal life history and under conditions favorable to the gametophyte even though the nuclei retain the sporophyte number of chromosomes. And it is possible that some of the aposporous developments in bryophytes and pteridophytes may be of this character. It is quite futile at present to carry this speculation further. What is desired is some cytological facts.

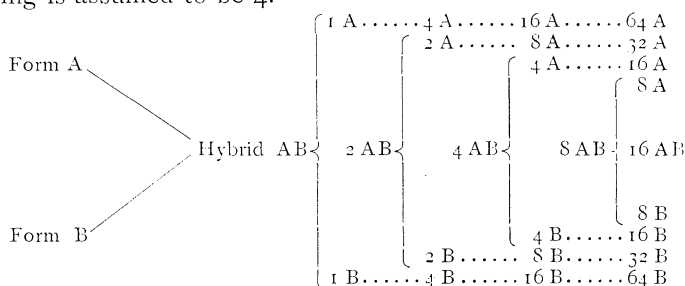
7. HYBRIDIZATION.

This is not to be a detailed discussion of the facts and theories of hybridization, a subject far too extensive for the purposes of our treatment. We shall only consider some of the bearings of the recent studies on fertilization and reduction phenomena upon the problems of hybridization treating it as a critical phase in the life history of the organisms concerned. Until recently the attempts to formulate definite laws for the formation of hybrids and their progeny upon a physical basis have not been satisfactory. But the work of a number of breeders all of whom owe their results in large part to a quick appreciation of Mendel's epoch-making contributions have brought much order out of what was a very confused subject. And accompanying the work of this group must be added the equally important conclusions of a number of cytologists whose investigations on the structure and behavior of nuclei in the critical periods of fertilization and chromosome reduction have done much to place Mendelian principles upon a cytological basis. We shall deal with the work of the latter group, for their contributions concern intimately the subject matter of these papers.

We shall not review the conclusions of Mendel except to point out the relations of some of his principles to cytological phenomena. The two papers of Mendel appeared in the proceedings of a natural history society of Brünn, Austria, under the dates 1865 and 1869. They lay buried until 1900 when De Vries, Correns, and Tschermak independently rediscovered them and called the attention of the scientific world to their worth. Soon after, Bateson published a translation of the two papers (*Mendel's Principles of Heredity*, Cambridge, 1902) with an introduction and a defense against the criticisms of Professor Wheldon. There have naturally been many reviews and short discussions of Mendelian theories and among them that of Castle entitled "Mendel's Laws of Heredity" (*Science*, vol. 18, p. 396, 1903) and Professor Bailey's "Lecture IV" in *Plant Breeding*, 1904, will perhaps give the reader the clearest and most concise statements.

The most striking feature of Mendel's investigations and those

of others, who have confirmed his conclusions, is the discovery in a number of animals and plants that the germ cells of the hybrid may be pure with respect to certain characters of the parents which are crossed. This principle is not without exceptions where the conditions are apparently complicated by unusual factors but the phenomenon when present is so striking as to command immediate attention and call for an explanation on a cytological basis. The purity of the germ cells of hybrids means in the words of Castle that "the hybrid, whatever its own character, produces ripe germ cells which bear only the pure characters of one parent or the other." Thus if two forms A and B are crossed the hybrid will have embodied in itself the characters AB, one of which however may lie latent, *i. e.*, may not be visible in the hybrid. Such a latent character when present is termed recessive while the prominent character is termed dominant. In a simple case some of the offspring of the hybrid AB will be found to have the character of A alone, some of them of B alone, and some of them will again have the mixed characters AB. If experiments are carried out on an extensive scale the proportions of these offspring from the hybrid may exhibit the remarkable fact that there are about twice as many forms of AB as either A or B, *i. e.*, the proportions of A's, AB's, and B's are in the ratio of 1 : 2 : 1. Furthermore the offspring of A when bred among themselves remain absolutely true producing a succession of pure forms all A's and the same results follow when the offspring of B are closely bred. But when forms with the mixed characters AB are bred with one another their offspring break up as before into three types A, AB, and B in numerical proportions expressed by the same ratio 1 : 2 : 1. The history is simply told in the following diagram where the number of offspring is assumed to be 4.



This remarkable proportion of forms derived from the hybrids AB, *i. e.*, A, AB, and B in the ratio 1 : 2 : 1 can only be explained on the assumption that the germ cells of the hybrid are pure with respect to the characters of either one or the other of the parents. The gametes from the hybrid, with the pure characters of either A or B and approximately equal in number, may unite with one another in three possible combinations AA, AB, or BB forming three types of offspring, one pure A, another mixed AB, and the last pure B. By the law of chance the proportions of these combinations (AA, AB, and BB) in a simple case will be in the ratio 1 : 2 : 1. This assumption of the purity of the germ cells of hybrids has been found to conform with the facts in a number of simple experiments where two characters such as A and B were sharply contrasted. When one of the characters in the hybrid is dominant and the other recessive the ratio can be expressed as D : DR : R as 1 : 2 : 1 which is merely a substitution of D and R for the characters A and B.

There are of course many factors which tend to modify the ratios as stated above and complicate the results. Thus the normal number of gametes may be of varying vigor and mortality so that there will be proportionately more or less of one type of fusion than is called for by the law of chance. Sometimes the characters of the parents remain evenly balanced in the hybrid and refuse to split up in the succeeding generations, remaining in a stable union in the germ cells produced by the hybrid. Such conditions prove exceptions both to the law of dominance and to that of purity of the germ cells. From these exceptions and particularly the last it is difficult to believe that any large proportion of the germ cells is *absolutely* pure, *i. e.*, bearing only the pure characters of one parent or the other. However, there is much evidence from our knowledge of the distribution of the chromosomes from one generation to the next, that certain relations are possible in the separation of germ plasm which approximate the ratios of Mendel's law and while rarely giving *absolutely* pure germ cells nevertheless do make possible a large proportion of *relatively* pure cells.

Let us examine now the chromosome history as a possible physical basis for the Mendelian principles. Such considerations

must rest on the assumption of what is termed the individuality of the chromosome. This means that the chromosome is believed to be a permanent organ of the cell which never loses its organic entity although the form may be frequently obscured, as in the resting nucleus, and which reproduces by fission during mitosis. We have given in other connections the evidence upon which the above view rests, evidence accumulated from the studies of the critical periods of gametogenesis, fertilization, and sporogenesis (with its reduction phenomena) in plants and of gametogenesis and fertilization in animals. All investigations indicate that paternal and maternal chromosomes maintain complete independence in the sexually formed cell or fertilized egg and in the mitoses of cleavage so far as these have been followed. Also, descendants of the chromosomes which became associated with fertilization have been recognized by their form at the end of the life history during the reduction phenomena of gametogenesis in certain animals (Sutton, :02, :03; Montgomery, :04) and of sporogenesis in the hybrids of *Drosera* (Rosenberg, :04a, :04b). Furthermore, the entire history of chromosome reduction in both animals and plants finds a satisfactory explanation only in the belief that descendants of maternal and paternal chromosomes are distributed as organic entities by the peculiar mitoses of this period.

There is a general agreement that the somatic chromosomes of animals and the sporophytic of plants become grouped in pairs to form bivalent structures before the heterotypic mitosis of the reduction division whether this be present in the primary gametocyte (animals) or the spore mother-cell (plants). The bivalent chromosomes (pairs of chromosomes, dyads) may become transformed into tetrads before the heterotypic mitosis by a division of each chromosome in the pair, as is characteristic of animals, or this division may be delayed until a somewhat later period during the heterotypic mitosis, as in plants. We are not concerned now with the dispute as to how the pairs of chromosomes come to lie side by side to form the bivalent structure or how tetrads are developed, activities which may indeed be various in different types and which will only be understood by a greater body of observations than we have at present (see dis-

cussion of "Reduction of Chromosomes"). The important point for us is the belief that the appearance of the bivalent chromosomes during reduction is due to the temporary union of somatic or sporophytic chromosomes in pairs and further that the reducing divisions distribute the members of the pair, which are believed to be descendants of the maternal and paternal chromosomes of the previous generation, as organic entities to the generation which is to follow.

It is difficult to overestimate the importance of this generalization. If the program prove to be correct as stated above and if the chromosome is established beyond doubt as a self-perpetuating organ of the cell and a bearer of hereditary characters we have then the possibility of studying the actual manner in which these structures are passed on from one generation to the next and perhaps determine the ratios or combinations through which the distribution is effected. The difficulty of making an exact determination of ratios in any form so far studied lies in our inability to distinguish the chromosomes of maternal and paternal origin. There is much evidence that the pairs of somatic and sporophytic elements, which form the bivalent chromosomes of the reduction mitoses of animals and plants respectively, are of different parentage but we do not know whether or not there is any rule in the arrangement of the pairs on the spindles of these mitoses although this is hardly to be expected. Cannon (:02, :03a) and others have held that the mitoses of reduction brought about the complete separation of the maternal and paternal chromosomes so that two of the resultant four nuclei contain chromosomes from one parent and two from the other, and the germ cells are in consequence *absolutely* pure in character. But this view was soon shown by Sutton (:03, p. 233; accepted by Cannon, :03b) to be at variance with the facts of breeding for if germ cells of hybrids are *absolutely* pure there could be no further change by cross-breeding and the first cross would be repeated over and over again without any divergence from the type, which is contrary to experience and fact. The pairs of chromosomes are probably arranged in every possible order and the maternal and paternal elements are distributed in every possible combination by the reducing

divisions. If this is true then by the law of chance the proportions of germ cells of the hybrid which are *absolutely* pure (containing chromosomes entirely from one parent) would be small. Likewise there would be a small proportion of germ cells in which the paternal and maternal chromosomes are equally distributed. And in contrast to these two groups the great majority of germ cells would have a marked preponderance of chromosomes derived from one parent or the other and this condition may be termed one of *relative* purity.

We shall now summarize the cytological evidence for the conclusions of the paragraph above, first with respect to the actual distribution of the somatic and sporophytic chromosomes as entities during the mitoses of reduction, and second as to the probability of the bivalent chromosomes consisting of a pair of maternal and paternal elements. The evidence on the first point has been treated as regards plants in our own account of "Reduction of the Chromosomes" and need not be repeated. With respect to the possibilities of distinguishing maternal and paternal chromosomes throughout a life history and especially at the period of chromosome reduction we must consider briefly the remarkably favorable studies of Sutton, Montgomery, Moenkhaus, Baumgartner, and Rosenberg.

Sutton (:02, :03) discovered in the "lubber grasshopper" (*Brachystola magna*) a form in which the somatic chromosomes, 23 in number, are markedly different in size, presenting a graded series with respect to pairs in which the two elements are approximately equal. There are then 11 types of chromosomes in two groups, a pair of each type, and in addition an accessory chromosome which remains apart from the rest in a special vesicle of its own. These two sets of 11 chromosomes appear with regularity throughout the mitoses leading up to the reduction divisions of spermatogenesis. Previous to the reducing divisions the chromosomes of each pair become closely associated end to end so that 11 threads appear which form 11 bivalent chromosomes (dyads) that later become tetrads through the division of each chromosome in the pair. Sutton concludes that the somatic chromosomes which make up each bivalent structure conjugate during synapsis and that the transverse fission which

appears during the formation of the tetrad simply separates the two somatic chromosomes of the pair, while the longitudinal fission is the usual division of chromosomes, appearing prematurely at this time. The conclusion is natural that the two series of the 11 pairs consist of maternal and paternal chromosomes which are distributed as organic entities by the reducing divisions. But there are no reasons for supposing that all of the paternal chromosomes will pass into one set of germ cells and all of the maternal into another but rather that the ratios of distribution will be by the law of chance according to which the great majority of germ cells will have a marked preponderance of chromosomes from one parent or the other, and will therefore be *relatively* pure. An exceedingly small proportion of germ cells may, by the law of chance, contain chromosomes entirely of maternal or paternal extraction, and an equally small proportion may contain 6 chromosomes of one parent and 5 of the other. The accessory chromosome divides but once during the mitoses of spermatogenesis so that two of the spermatozooids have 11 chromosomes and two 12. No accessory chromosome appears in the mitoses of oögenesis indicating that the female insect lacks this structure which confirms the belief of McClung (:02) and others that the accessory chromosome is a determinant of the male sex.

Montgomery in a series of studies upon insects and Amphibians, which are summarized in a recent paper (:04), reached conclusions in striking support of the theories of the individuality of the chromosomes, the association of pairs of chromosomes during synapsis to form bivalent structures and the probability of the elements of each pair (bivalent chromosomes) being of maternal and paternal origin respectively. His results on the last point are of especial interest in relation to hybridization. In a large number of insects, chiefly Hemiptera, Montgomery has found pairs of chromosomes, which he terms heterochromosomes, much smaller or much larger than the others and these may be followed through mitosis from one nucleus to another. The heterochromosomes of each pair are known to unite with one another during synapsis to form the bivalent chromosomes of the reduction mitoses and they then become separated, each

dividing once, so that every germ cell receives a single heterochromosome of whatever sort. Fertilization then brings the heterochromosomes together again in pairs until the next period of chromosome reduction. This history is then parallel to Sutton's account of the lubber grasshopper (*Brachystola*), the difference being that the latter form presents a remarkably graded set of paired chromosomes. Montgomery regards the small chromosomes and the accessory chromosome as structures tending to disappear in a process of evolution from a higher chromosomal number to a lower.

Moenkhaus (:04) crossed reciprocally two species of fishes (*Fundulus heteroclitus* and *Menidia notata*) and obtained hybrid embryos which reached an advanced stage of development. The chromosomes of the parents are readily distinguished by size and form. These chromosomes were followed throughout the development of the hybrid embryo and were found to retain their peculiarities so that the two sets may be easily separated in favorable tissues. This investigation furnishes some of the strongest evidence of the individuality of the chromosome and the complete independence throughout the life history of the two sets derived from each parent. Could these hybrid embryos be raised to maturity we should expect to find during spermatogenesis and oögenesis an association of the chromosomes in pairs, those of paternal extraction with those of maternal to form the bivalent chromosomes preliminary to the reducing divisions, and a distribution to the sexual cells in varying proportions which would, however, give a very large ratio of *relatively* pure germ cells.

Baumgartner (:04) in studies upon spermatogenesis in the cricket (*Gryllus*) was able to distinguish the chromosomes by their form, following them through the mitoses of reduction. Most of the chromosomes have the form of straight or bent rods but there are apparently two rings in each set in *G. domesticus*. The variation in the form of chromosomes in the nucleus is well known but it has not been supposed that a definite form might be characteristic of an element and be maintained throughout the successive mitoses of a life history as seems probable from Baumgartner's results.

Rosenberg's (:04a, :04b) studies on hybrids of *Drosera rotundifolia* (with ten chromosomes in the gametophyte) and *D. longifolia* (with twenty chromosomes) offer clear evidence that the chromosomes which unite in pairs to form bivalent structures preliminary to the reduction phenomena of sporogenesis are of different parentage. The sporophyte number of chromosomes in the hybrid is thirty, as would be expected. The reduced number appearing at the first mitosis of sporogenesis is, however, not fifteen but twenty chromosomes, ten of which are plainly double the size of the other ten. The explanation of this interesting condition is that the ten chromosomes of *D. rotundifolia* unite with one half of the twenty chromosomes of *D. longifolia* giving ten large bivalent structures accompanied by the ten chromosomes of *D. longifolia* which are without mates. This explanation finds clear support in the facts that the chromosomes of *D. rotundifolia* are larger than those of *D. longifolia* and that the bivalent structure consists of a larger and a smaller element thus giving clear evidence that the pairs of chromosomes which unite in *Drosera* are of different parentage. The single chromosomes which are without mates may pass to one or the other of the poles of the spindle or may be left behind when the daughter nuclei are formed.

This group of investigations illustrates very clearly the character of the evidence that is leading many biologists to assign to the chromosomes the functions of bearing and distributing hereditary characters. The question at once comes up as to whether or not the chromosomes may differ among themselves to a greater or less extent even in the same species or individual. Montgomery, Sutton, with others, have established a difference in the *size* of chromosomes. Baumgartner distinguishes differences in *form* in the same species and the studies of Moenkhaus and Rosenberg have shown that the chromosomes of different parents may retain their peculiarities of *form* in hybrids and be really separated. To these investigations should be added the recent conclusions of Boveri (:02, :04), that chromosomes actually differ in *function*. Boveri found that the chromosomes of eggs of echinoderms that were fertilized by two or more sperms are distributed by multipolar spindles to a varying number of

blastomeres which in consequence received a varying number and assortment of chromosomes. Boveri then separated these blastomeres and followed their independent development into larval stages which exhibited marked differences in form that could be correlated with the irregularities in the number of chromosomes contained in each, thus suggesting that specific chromosomes have specific functions. With this sort of evidence accumulating from both the morphological and physiological side it is not surprising that many biologists believe that specific characters are actually held or are controlled by chromosomes or groups of chromosomes.

Such views of course presuppose that the chromosomes retain a high degree of independence of one another and that variation is expressed chiefly through different combinations of chromosomes and not by modifications of the chromosomes themselves. Yet there is strong evidence of an actual mixing or interchange of the idioplasm among the chromosomes. This possibility which is of course contradictory to the view of the *complete* independence of the chromosomes finds its chief support in the close association of the pairs of chromosomes with the organization of the reduced number of bivalent structures during synapsis. These pairs have been reported so intimately united as to be actually fused. Allen (:05) has described for *Lilium* the union of two sets of chromomeres, one believed to be derived from a paternal spirem and the other from a maternal, which come to lie side by side during synapsis and unite to form a spirem with a single series of fusion chromomeres. This single (fusion) spirem later splits longitudinally and the two halves are regarded as again representing maternal and paternal spirems but there are evidently opportunities during the period of fusion for significant reciprocal interaction between the two idioplasms. This conception of the fusion of idioplasm from the two parents is an old view which has been held by such well known biologists as Hertwig and Strasburger.

De Vries (:03) has recently discussed the significance of the pairing of chromosomes before the heterotypic mitosis in relation to the theory of pangenesis. He conceives the paternal and maternal chromosomes as coming together during synapsis in

homologous pairs so that corresponding pangenes or groups of pangenes are brought together and that there may be a mutual interchange or transfer of idioplasm with the result that the chromosomes after separating may contain a mixed set of pangenes although each is supposed to have a complete assortment. The interchange makes possible all forms of combinations of the pangenes in the two sets, according to the laws of chance, which might be expressed in proportions that would approximate in some cases the ratios of Mendel. If the parents are widely different from one another their idioplasm may not correspond sufficiently to make possible this union and interchange of pangenes so that the process is suppressed and the hybrid is sterile.

Allen (:05, p. 247) points out that the union of two spirems during synapsis with the fusion of two sets of chromomeres, according to his account of the lily, offers a number of possibilities with respect to the constitution of idioplasm following the reduction mitosis. (1) There may be such a fusion of elementary units that a single idioplasm is formed different from either parent which would of course be distributed equally to the reproductive cells by the subsequent double longitudinal fission of the single (fusion) spirem. This would be expected to give hybrids of much the same form in every instance and these would remain stable (constant). (2) There may be a greater or less mixing or modification of units but without the actual union and formation of a new idioplasm in the hybrid. Then by the splitting of the single (fusion) spirem there might result a distribution of the mixed idioplasm following ratios or proportions approximating Mendel's law. (3) There may be in part a fusion and in part a mixing of idioplasm which would be expected to result in a varied combination of parental characters in the offspring. (4) While the chromosomes may be distributed according to ratios similar to Mendel's principles their respective characters may be greatly modified by their temporary union during synapsis. (5) Portions of the idioplasm may interact upon one another so that when they are separated by the reduction mitoses their character has become variously modified. (6) Finally, Allen, of course, recognizes the possibility that parental

idioplasm may be separated so purely by the longitudinal splitting of the single (fusion) spirem or through the distribution of unmodified sporophytic or somatic chromosomes as to give *absolutely* and *relatively* pure germ cells through Mendelian laws.

Allen's discussion, very briefly summarized above, is important for the emphasis which is laid upon the significance of a possible mixing of the parental idioplasms in the more or less complete union of chromatic material, which is generally recognized as characteristic of synapsis. There is a general tendency to rest content when the chromosomes are accounted for as units while they are merely the grosser form of expression of the idioplasm whose final architecture is intricate far beyond our present powers of analysis. Allen's own studies upon the events of synapsis in the lily with the regular fusion in pairs of chromomeres of different parentage may well cause one to hesitate in a full acceptance of the chromosome as fixed and unchanged in its organic constitution throughout the life history. The phenomenon of hybridization is far too complex to be explained in terms of simple ratios and while some characters may be paired or correlated in proportions that can be expressed by mathematical formulæ there is little probability that the assemblage of characters which make the species can be so definitely grouped as the strongest disciples of Mendel may hope. However, a great forward step has been taken and we may expect important results from the empirical methods so clearly defined by Mendel and by the close investigation that cytologists are making of the history of idioplasmic structures (chromosomes) during ontogeny.

8. XENIA.

Xenia is the "immediate or direct effect of pollen on the character of seeds and fruits." The term was first proposed by Focke, in 1881, and is now well established. Xenia has long been known to the plant breeder as one of the most interesting and puzzling problems of hybridization. The botanist has naturally looked for the results of hybridization in the development of the embryo from the seed since this structure has received

the substance of the sperm nucleus of the male parent. But facts have clearly shown that the pollen may also affect the structure of the endosperm in the seed as well as cause the development of the embryo. Since the endosperm holds no genetic relation to the embryo it has seemed very remarkable that it should take on hybrid qualities. It has also been claimed that other regions of the seed or fruit, such as portions of the pericarp were also affected, but it is doubtful whether this is really so or at least whether such changes are truly a feature of the protoplasmic structure and thus deeply seated in the organism as a feature of hybridization.

It is only within recent years that a satisfactory theory has been suggested for the influence of pollen outside of the embryo. And this explanation rests on the discovery of the activities of the second sperm nucleus which enters the embryo-sac and which is known in some cases to unite with the polar nuclei constituting a triple nuclear fusion within the sac that is generally known as "double fertilization." We have briefly referred to the phenomenon in the latter part of the account of "Asexual Cell Unions and Nuclear Fusions" in Section IV and shall take it up now in greater detail. The best account of xenia is a very clear treatment by Webber, in 1900.

The explanation of xenia upon the facts of "double fertilization" was proposed almost simultaneously by De Vries ('99, :00), Correns ('99b), and Webber (:00). Double fertilization was first observed by Nawaschin ('98) in *Lilium* and *Fritillaria* and shortly after was described in greater detail by Guignard ('99b) in other species of the same genera and in *Endymion*. Since these discoveries the phenomenon has been reported by a number of investigators in many other forms representing widely divergent groups in the Monocotyledonæ and Dicotyledonæ and there is every reason to believe that it is widespread in the angiosperms. A review of the recent literature is given by Coulter and Chamberlain (*Morphology of the Angiosperms*, 1903, p. 156). There is no fixed order in the events of the triple nuclear fusion of "double fertilization." The polar nuclei may have united at the time when the pollen tube enters the embryo-sac, in which case the second sperm nucleus coalesces with an organized fusion

endosperm nucleus. Or, the two polar nuclei and the sperm nucleus may all three fuse together practically simultaneously. And again the sperm nucleus may unite first with one of the polar nuclei and the second be drawn later into the triple fusion. But no cases seem to have been reported in which but one polar nucleus unites with the sperm leaving the other free although such a combination may be expected. Also, no one has observed an independent division of the sperm nucleus within the endosperm, although as we shall see, there are reasons for believing that such a development may sometimes take place.

We have already given in Section IV the reason why these triple nuclear fusions may be kept apart from sexual phenomena since we have no knowledge of the phylogenetic history of the processes involved. It seems best at least for the present to regard the phenomenon as a special development associated with the peculiar and highly specialized conditions within the embryo-sac. This detailed and highly difficult problem of phylogeny has no especial bearing on the physiological features of xenia with which we are at present concerned.

The best understood examples of xenia are found in the hybrids of maize and are clearly described in the very interesting paper of Webber (:00). As is well known, some of the varieties of corn are distinguished among other characters by the color of the kernels, which are blue, red, yellow, and white, and also by the surface, which is smooth in the starchy corns (flint or dent) and wrinkled in the sugary sweet corns. When well marked pure races are grown out of reach of chance cross-pollination, the offspring remain true to their seed characters but it has long been known that the varieties of corn hybridize very readily so that when grown close together the ears will very frequently present seeds mixed as to color and texture. Thus when exposed to cross-pollination a corn which is characteristically yellow or white may bear blue or red kernels or a form with wrinkled and starchy kernels may develop smooth starchy corn if varieties with these characters are in the vicinity. The color character is known to lie in these examples in the outer layer of the endosperm (aleurone layer) and of course the food material whether prevailing starch or sugar, which gives the

surface a texture smooth or wrinkled, is stored within the endosperm.

The clearness of xenia in the maize has led to a number of careful studies on cross-pollination beginning with the work of Vilmorin (1866), Hildebrand (1867), and Friedrich Körnicke (1872). The possible explanation of xenia in maize through "double fertilization" which introduces qualities of the male parent from the pollen into the endosperm was suggested by experiments of De Vries on hybridizing maize in the summers of 1898-99 and Correns and Webber in 1899. De Vries ('99, :00) pollinated a wrinkled-seeded sugar corn from a variety of smooth starchy corn and obtained smooth starchy kernels which when cultivated in the succeeding summer were found to be true hybrids. He concluded that this furnished experimental proof that the endosperm of the sugar corn was affected by the entrance of a sperm nucleus from the starchy variety according to the theory of "double fertilization" proposed by Nawaschin ('98).

Correns ('99b) in the same year expressed similar conclusions in a clear statement of the theoretical aspects of the problem of xenia as found in *Zea mays*. Correns advanced a number of propositions some of which should be noted for their speculative interest. Thus he states (proposition 7) that the influence of the new pollen (*i. e.*, from the male parent of the hybrid) is expressed as xenia only in the endosperm and (proposition 8) only in the pigment present or the chemical nature of the reserve material whether starchy or sugary. If the two races differ only in the presence of one character, as in the color of the aleurone layer, that character is only found in xenia when brought by the pollen (proposition 10). Xenia is then only expressed in a hybrid (proposition 14) by the formation of a pigment which the race of the female parent does not possess or of a more complicated chemical compound (such as starch) in place of a simpler (as dextrin). Correns (:01) later presented in a lengthy paper, beautifully illustrated, the full results of his studies on xenia in maize with a discussion of the hybrids.

Webber (:00) also simultaneously with De Vries and Correns conducted extensive experiments in hybridizing a number of

varieties of corn distinguished by the color of the kernels, which were white, yellow, red, or blue and by the texture whether smooth, hard, and starchy (dent or flint corn) or wrinkled and sugary (sweet corn). The results of his investigation are admirably presented with excellent illustrations. He found that the smooth kernel and starchy endosperm of the dent and flint corn were transmitted very conspicuously as *xenia* when these forms were employed as the male in crossing with the sweet corns whose kernels are wrinkled and sugary. The characters of the sweet corns do not seem to be expressed as *xenia* when smooth, starchy, dent corn is used as the female member of the hybrid. This experiment would seem to support Correns' proposition number 14 that a more complicated compound is always formed in *xenia* in place of a less complex. But Webber found that flint corn, which is smooth and starchy, when pollinated with a form of sweet corn developed the wrinkled kernel and sugary type of endosperm of the male member indicating that this rule of Correns is not universal. And McClure ('92) obtained similar results in crossing a white dent race with pollen of Black Mexican which is a sugar corn with black kernels. The product in this case showed *xenia* clearly in having the wrinkled blue-black kernels of the male sugar corn.

Some of Webber's most striking results were obtained in pollinating yellow and white corns with blue-black and red races. The color was transmitted as *xenia* in a most striking manner. Webber agrees with other authors that the color is only present in the endosperm of the kernels. Thus the red of certain dent corn, which lies in the pericarp, is not passed on as *xenia* and McClure observed the same facts in experiments with cranberry corn whose color lies in the seed coat and is not transmitted when employed as the male member in crossing with white corns. Webber's experiments show, as do those of other investigators, that the absence of color in the kernels of the male parent does not seem to affect the tint of the kernels when the female is markedly colored, in agreement with Correns' proposition number 10. But Webber is not convinced that some influence might not be exerted on colored corn when pollinated from races with colorless endosperm, because of certain experiments on variegated *xenia* which will be described presently.

These experiments of De Vries, Correns, Webber, and others have established experimentally the facts of xenia and Nawaschin's theory of double fertilization seems to offer the only explanation of the phenomenon. But it was left to Guignard (: 01) to make the concluding observation that a second sperm nucleus does actually enter into the composition of the endosperm of maize, and this fact clinched the argument which up to this time had been a speculation.

Webber has made a very important addition to the theory of "double fertilization" as an explanation of xenia in some observations and speculations on a mottled condition which is sometimes present when white corns are pollinated by colored. He found that the color was sometimes only transmitted in spots as when Hickory King was pollinated by Cuzco, or perhaps only half a kernel may be colored. Webber offers the hypothesis that the second sperm nucleus may enter the embryo-sac but instead of uniting with the two polar nuclei to form a triple fusion may itself divide separately and thus gives rise to a progeny very different from the other endosperm nuclei. There might then be two sets of nuclei in the endosperm one of which is composed of nuclei which would come directly from the male parent. These latter then might become distributed throughout the embryo-sac but would tend to remain in groups as multiplication progressed and would certainly be expected to influence the character of the tissue which is formed later when the walls are developed around the free nuclei. As Webber expresses it, there might be formed islands of tissue in the endosperm whose cells contain nuclei derived directly from the second sperm and such tissue would be expected to show characters of the male parent in spots as xenia. Again, if the sperm nucleus should unite with only one of the polar nuclei and the other should give rise to an independent progeny we should expect similar mixed conditions in the endosperm, with xenia only expressed in the areas dominated by nuclei containing material derived from the sperm.

There have been reported illustrations of xenia in tissues outside of the endosperm but we are fully justified in awaiting their confirmation before accepting them, especially since some

have failed to stand the test of critical investigation, in the light of the present theory. Thus certain investigators have reported xenia in the color of the seed coats of certain peas. But Giltay ('93) in a series of experiments found no instance where color was transmitted to these tissues. The pigments in these plants lie in the cotyledons of the embryo which of course are readily visible through the thin coats of the seed. While the present theory of xenia is very recent and has been critically applied in few forms, it seems thoroughly satisfactory in every particular with no clearly established evidence against it.

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